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Review

Implication of evolution and diversity in arbuscular and ectomycorrhizal symbioses☆

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ABSTRACT

Being highly sensitive to ecological variations, symbiotic associations should inherently have a limited occurrence in nature. To circumvent this sensitivity and reach their universal distribution, symbioses used three strategies during their evolution, which all generated high biodiversity levels: (i) specialization to a specific environment, (ii) protection of one partner via its internalization into the other, (iii) frequent partner exchange. Mycorrhizal associations follow the 3rd strategy, but also present traits of internalization. As most ancient type, arbuscular mycorrhiza (AM) formed by a monophyletic fungal group with reduced species richness did constantly support the mineral nutrition of terrestrial plants and enabled their ecological radiation and actual biodiversity level. In contrast ectomycorrhiza (EM) evolved later and independently within different taxa of fungi able to degrade complex organic plant residues, and the diversity levels of EM fungal and tree partners are balanced. Despite their different origins and diversity levels, AM and EM fungi display similar patterns of diversity dynamics in ecosystems. At each time or succession interval, a few dominant and many rare fungi are recruited by plants roots from a wide reservoir of propagules. However, the dominant fungal partners are frequently replaced in relation to changes in the vegetation or ecological conditions. While the initial establishment of AM and EM fungal communities corresponds to a neutral recruitment, their further succession is rather driven by niche differentiation dynamics.

Contents

Introduction

The term symbiosis was introduced in the last quarter of the 19th century to define tight associations between two organisms belonging to different taxa (de Bary, 1879; Plaisance et al., 2011). The initial view of De Bary encompassed all combinations of the three possible interaction effects on each of the partners, i.e. (+) beneficial, (0) neutral or (−) detrimental (de Bary and Balfour, 1887). In the meantime however, only mutualistic associations that are beneficial for both partners (+/+) are considered as symbioses, even though some schools also include parasitism (+/−) (Douglas, 1994). In fact only these two types of interactions fulfill the tightness requirement given in the definition, which is not the case for commensalism (+/0), amensalism (−/0), neutralism (0/0) or of course antagonism (−/−), in which at least one of the partners has a loose or even no real direct association to the other one.

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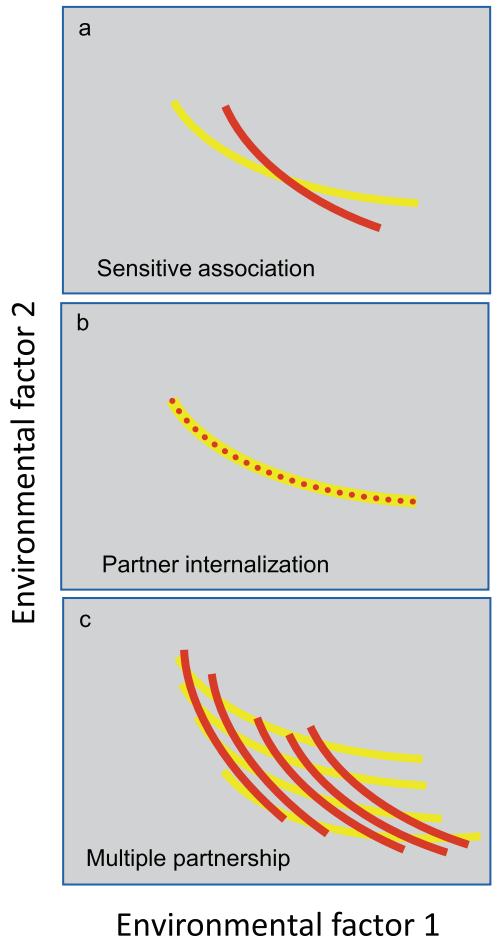

Fig. 1. Schematic representation of performance isoclines (lines of equal performance) of different species in relation to the variations of two environmental factors. The three graphs illustrate the three possible strategies used by symbiotic associations to cope with the predicted instability of tight symbiotic associations face to changing ecological conditions: (a) sensitive association only adapted to narrow specific ecological conditions; (b) internalization of one partner that is than protected by its host faced to changing ecological conditions; (c) frequent partner changes as reaction to changing ecological conditions.

The symbiosis concept was long difficult to handle in the field of theoretical ecology (Boucher, 1985). The problem largely relies on the difficulty to figure out how two distinct organisms with different growth and reproduction dynamics and with specific performance answers to variations of ecological factors might maintain their association in a balanced equilibrium faced to changing environmental conditions. One of the simplest illustrations of this conceptual theoretical difficulty is given by plan representations of performance isoclines. Such isoclines represent as lines the combinations in variations of two different environmental factors that enable the performance of one organism to be constant. If we take as example pH and phosphorus concentration in a soil as environmental factors and plant growth as measured performance, the isocline would figure out which combinations of pH values and P-concentrations produce a similar plant growth level. Models based on plan representations of performance isoclines predict that two different species inherently have distinct isoclines with at best only one or a few intersection points (Fig. 1a). Because the performance answer of the two partners of a symbioses to changes in environmental conditions are not similar, the model predict that symbiotic associations should only be stable under very narrow environmental conditions, be sensitive to any ecological variations, and therefore be rare (Boucher, 1985). However, considering the profusion and frequency of symbiotic associations observed in all kinds of habitats of our planet, it must be concluded that ecologists probably simply long failed to draw the proper consequences from a right theory. In fact the theory does nothing else than pin pointing the specific environmental pressure exerted on symbiotic systems. However, these have developed different mechanisms to meet this challenge (Douglas, 2008). Here we propose to order these mechanisms into three categories of strategies, which all contributed to generate remarkable levels of biodiversity. The *first strategy* consists in conforming to the theory and to in fact be sensitive to environmental variations (Fig. 1a). This model is followed by symbioses such coral reef inhabiting symbiotic associations, which are indeed extremely sensitive to variations in the quality of water, (Conti and Cecchetti, 2001; LaJeunesse et al., 2010). As a consequence of this sensitivity, coral reefs consist in a huge diversity of niches, which results in one of the highest biodiversity hotspot in oceans (Plaisance et al., 2011). The *second strategy* consists in suppressing the direct contact to the changing environment for one of the symbiosis partners through its internalization into the second one (Fig. 1b). This strategy is encountered in true endosymbioses such as chloroplasts and mitochondria (see Büchel, 2015; Kroth, 2015), but also in nitrogen fixation nodules formed by bacteria and plants (see Gresshoff et al., 2015), in the gut microbiomes of diverse types of animals, or even in light producing organs of several terrestrial and aquatic metazoa (see examples in Douglas, 1994). This strategy resulted in the evolutionary acquisition of diverse genetic, physiological and anatomical traits including specific sophisticated organs to "protect" the internalized partner and warrant optimal physiological conditions for its functioning (Toft and Andersson, 2010). As a consequence, this strategy profoundly impacted the evolution of the organisms involved in such symbiosis types and also generated a high level of biodiversity (Ley et al., 2008). The *third strategy* simply consists in frequently changing the symbiotic partner when environmental conditions change (Fig. 1c). This is the case in lichenized symbioses between fungi and algae or cyanobacteria, for which the fungal partner increases its geographical range and ecological niche by associating to adapted photobionts in different climatic regions (Fernandez-Mendoza et al., 2011). The authors pinpoint that together with isolation by distance, partner shifts lead to genetic isolation between population and drives evolution. Finally this strategy resulted in producing a high level of biodiversity as illustrated by the inventory of a least 18,000 lichen "species" occupying all types of habitats under a wide range of climates (Feuerer and Hawksworth, 2007). Lichens also illustrate that the three strategies presented can be combined within a given symbiosis. Together with their sensitivity to air pollution, their potential to use wide distance propagation via vegetative propagules to colonize similar substrates over wide geographical range pleads for ranging lichens also under the first strategy.

This article focuses on mycorrhizal symbioses between plants and fungi, in which each organism is not only associated to different partners at a given time, but also changes the partner spectrum both in time and space. However, in some types of mycorrhiza or at given phases of the association in some cases, the fungi are internalized in plant cells, so that mycorrhiza combine the second and the third presented strategies. By considering the dominant two kinds of mycorrhiza, the article explores the consequences of this combined strategy in terms of natural history as well as functional and structural biodiversity including its dynamics in time and space.

Natural history of mycorrhizal symbioses

The term mycorrhiza was coined in the last part of the 19th century to design symbioses between plant roots and soil fungi (Smith and Read, 2008). Soon it was recognized that the mycobionts

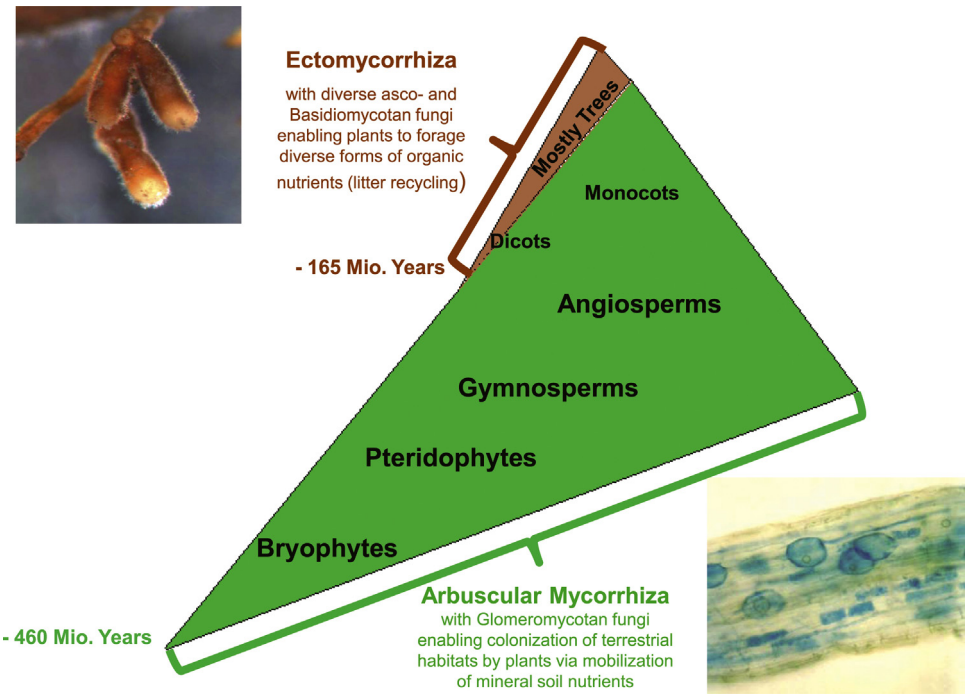

Fig. 2. Summary of the natural historical development of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) symbioses in relation to the ecological radiation of terrestrial plants. While the oldest type, the AM gave rise to a wide diversification of plants by supporting their mineral nutrition, the more recent type, the EM are partners of a limited diversity of tree species, but they enable them recycling of organic nutrients.

(fungal partners) help the phytobionts (plant partners) to better forage and acquire soil resources (nutrients and water), while the photobionts deliver photoassimilates to the mycobionts (Buscot et al., 2000). Further functions of mycorrhiza are an enhanced resistance against biotic and abiotic stresses. Fossil records indicate that the initial type of mycorrhiza was formed 460 million years ago (Redecker et al., 2000), which corresponds to the onset of the colonization of terrestrial habitats by plants (Fig. 2). The fungal partners of this most ancient type of mycorrhiza all belong to the Glomeromycota, a taxonomical group recently erected as a distinct phylum within the true fungi besides the Zygo, Asco- and Basidiomycota (Schüßler et al., 2001). All members of the Glomeromycota are obligate biotroph mycorrhizal symbionts on plants, except one taxon associated to blue algae (Schüßler et al., 1994). The main aptitude of glomeromycotan fungi is the mobilization and transport of mineral nutrients (particularly phosphorus) from soil micro-compartments that are not accessible to roots and even root hairs (Karandashov et al., 2004). This property was probably crucial for enabling plants to move from an aquatic environment, in which nutrient resources are directly available, to terrestrial habitats in the soil of which depletion zones rapidly develop after element absorption by organs such as roots (Corradi and Bonfante, 2012). As a mirror of their strategic importance for mineral absorption, Glomeromycota have remained associated to plants during the whole evolution and diversification of bryophytes over pteridophytes to gymno- and angiosperms, including dicots and monocots (Wang and Qiu, 2006). About 80% of the today plants are associated to Glomeromycotan fungi, which penetrate into their root cortex and first grow intercellular before forming highly branched haustoria-like intracellular structures called arbuscules (Karandashov et al., 2004). This trait led to call these mycorrhiza "arbuscular mycorrhiza". The arbuscules are the main site of the exchange of phosphorus and further minerals mobilized by the thin fungal hyphae exploring the soil. In contrast, the photoassimilate transfer to the mycobiont mainly occurs in the intercellular interface of the roots (Smith and Smith, 1990). The ecological radiation of AM-plants led to enhance plant diversity (Corradi and Bonfante, 2012), but also to a dramatic primary production increase corresponding to the evolution of larger plants such as trees. To support the enhancement of plant size and anatomical complexity, a diversity of structural and functional plant molecules (e.g. lignin) appeared. The difficult to degrade tissues and compounds resulting from this evolutive differentiation represented new resources, which in turn triggered the evolution of decomposing brown and white rot fungi within the Asco- and Basidiomycota, which can produce exoenzymes capable of mineralizing complex substrates (Eastwood et al., 2011). Recent phylogenetic analyses support the view that formation of coal from huge amounts of accumulated plant residues was probably dramatically reduced after this group of decaying fungi evolved and triggered decomposition (Floudas et al., 2012).

There are phylogenetical evidences that within distinct white and brown rot fungal lineages, the aptitude to form a secondary type of mycorrhiza emerged and was sometimes lost again within different taxa of white and brown rot fungi in the last 125 million years (Bruns and Shefferson, 2004). This secondary type is called ectomycorrhiza (EM) and is encountered on roots of major forest tree species in the boreal and temperate regions and also on some tree taxa of the tropics (Fig. 2, Smith and Read, 2008). Mycobionts of EM form hyphal mantels around the tip of short absorbing roots, and from there, they colonize the apoplast of the root cortical parenchyma to form an aposition structure called the "Hartig net", where the exchange of soil nutrients against photoassimilates takes place (Blasius et al., 1986). Even though they lost copies of genes encoding extracellular enzymes compared to their white and brown rot fungal ancestors, EM mycobionts have a broad repertoire of degrading enzymes (Plett and Martin, 2011), which enable them to mobilize resources, in particular nitrogen and phosphorus, from a variety of mineral to organic substrates, including rock, plant litter and coarse wood debris. In the latter case, EM fungi contribute to a kind of short cut in the nutrient cycling, whereby they enable their host plants to remobilize resources from their

own dead matter without a complete mineralization via further microorganisms (Read and Perez-Moreno, 2003). Additional types of mycorrhiza evolved within specific plant taxa such as Ericaceae and Orchidaceae including achlorophyllous plants (Smith and Read, 2008), these types of mycorrhizas that will not be considered in this article are typical endomycorrhiza, in which a large part of the fungal colony growths inside plant cells. Arbuscular mycorrhiza are also considered as endomycorrhiza, because the mycobiont is completely internalized in root tissues at an initial stage, and the mycelium only starts exploring the soil compartments after a large number of arbuscules have been established. In contrast in ectomycorrhiza the largest part of the fungal colony grows outside of the roots.

Balance between partner diversity in arbuscular and ectomycorrhiza

Global plant species richness diversity is in the order of several hundred thousand taxa and most of them are arbuscular mycorrhizal (Wang and Qiu, 2006). In contrast, only some 300 species of AM mycobionts have been described based on morphological criteria (Öpik et al., 2013). The diversity of AM mycobionts is difficult to estimate, as Glomeromycota do not display any sexual reproduction, and no good species concept exists (Corradi and Bonfante, 2012). Based on multi-sequence polymorphism within of the rDNA region it can be estimated that there are perhaps 10 times more Glomeromycota species than actually described morphospecies (Krüger et al., 2012). Even on the basis of this estimation, the species respective richness of AM plants and AM fungi differ by two orders of magnitudes. Within EM symbiosis, the situation is completely different as species richness of tree and fungal partners is in the same order of magnitude, ca. 6000 species, respectively (McGuire et al., 2013; Tedersoo et al., 2010). The limited species richness of AM mycobionts may reflect their monophyletic origin and the absence of sexual reproduction, while the numerous asco- and basiomycetous EM fungi have a polyphyletic origin and all display sexual reproduction. However, this provides no rational explanation to interpret the fact that the disbalance between the diversities of photo- and mycobionts are inverse in AM compared to EM symbioses (see discussion in (Allen et al., 1995). However, it can be noticed that EM fungi forage more diversified heterogeneous soil resources than AM fungi do (Buée et al., 2007), which can explain their higher diversity. Even though AM fungi are detected on complex organic substrates such as litter (Kottke et al., 2004), there is no proof that they can directly attack these substrates. Rather, they suck the mineralization products resulting from the activity of further microbial decomposers and make them available to their photobionts (Hodge and Fitter, 2010). Why the EM plant diversity is lower than the one of AM plants is also unclear. This discrepancy is not related to the fact that EM are almost exclusively formed on trees, because AM also form on trees, and AM trees display a higher species diversity than the one of their AM mycobionts (Alexander and Lee, 2005). This enigma is also underlined by the fact that EM dominated forests always display a limited tree diversity including those that develop in the tropics, a plant biome in which AM dominated forests display an extreme high tree species richness (Alexander, 2006). Vice versa, AM dominated plant communities often display high plant diversity, although the diversity of AM fungi is low compared to the one of EM mycobionts (Read and Perez-Moreno, 2003).

Fungal diversity patterns in AM and EM

The recent development of molecular techniques has opened avenues for exhaustive inventory of diversity and species composition patterns of fungal partners of both EM and AM. In particular studies based on next generation sequencing detect higher levels of mycobiont diversity per plot than all other approaches (morphotyping, trapping, Sanger sequencing) (Öpik et al., 2013). However, the increased exhaustiveness of NGS based studies did not change the frequency distribution patterns found in former studies. This universal pattern follows a typical harp shaped distribution, where only a few fungal taxa are detected with high frequency, while there is a long list of mycobionts with rare occurrence (Husband et al., 2002; Kaldorf et al., 2004). However, even though repeated time series investigations are rather rare, there are solid indications of shifts in the dominant mycobiont taxa in relation to seasonal variations (Dumbrell et al., 2011) and plant succession (Bennett et al., 2013; Peay et al., 2011). The harp shaped mycobiont frequency pattern suggests that the plant cover present in each ecosystem traps a limited set of partners providing the best adaptation to the local ecological conditions. As they receive photoassimilates from their phytobionts, these selected partners increase their biomass, growth and further root colonization performance, which reinforces their dominancy probability (Helgason et al., 2007), even though preferential specificity between partners tends to maintain diversity (Vandenkoornhuyse et al., 2003). However, the time related changes in the dominant mycobiont species indicates the instability of their association with plants, as predicted by the ecological theoretical view on symbioses. The succession within the dominant mycobionts might reflect shifts in the vegetation composition and function (photosynthesis efficiency, nutrient requirements), but also changes in the niche partitioning in the soil environment (Bruns, 1995). To unravel these mechanisms still requires numerous monitoring and experimental studies.

Recruitment and diversity dynamics of mycobionts in plant communities

The observed succession shifts in mycobiont populations requires that there are available propagules in form of spores, infected roots or free living mycelium within the soil. Recently, it was shown that the mycobiont diversity found in soils is indeed higher than the one found on roots engaged in symbiosis, pin pointing that soil is a reservoir of mycobiont partners for plants (Hempel et al., 2007). A field experiment has demonstrated that this reservoir consists of propagules present in soil and awaiting their recruitment, but it is also enriched by the import of additional propagules from neighbor or distant plots (Kaldorf et al., 2004). This propagule import is surely of crucial importance to maintain a reservoir of adapted mycobionts (Peay et al., 2011). In native soils found after glacier retirement, volcano eruptions or major environmental disturbance (Renker et al., 2004, 2005), the pioneer plants are often non-mycorrizal (Fig. 3), and they are replaced by mycorrhizal species only after the import of mycobiont propagules by wind or animals (Allen et al., 1992). In already developed ecosystems, there are indications that stable plant covers select only a limited amount of adapted mycobionts from the propagule pools present in the soil (Fig. 3, Johnson et al., 2003). Without permanent propagule import, and the above mentioned succession in the active mycorrhizal fungal partners, this should tend to reduce the mycobiont diversity in old plant communities.

Many of the actual investigations on mycobiont biodiversity address the relationship between species richness of both partners of mycorrhizal symbioses. In general, field experiments in which the plant species richness is manipulated find positive correlations between the species richness of photo- and mycobionts (Scherber et al., 2010). However, it must be pointed out that most of these experiments analyze rather young vegetation communities, and cannot reflect the situation in older established ecosystems. In addition, in manipulative plant biodiversity experiments, the

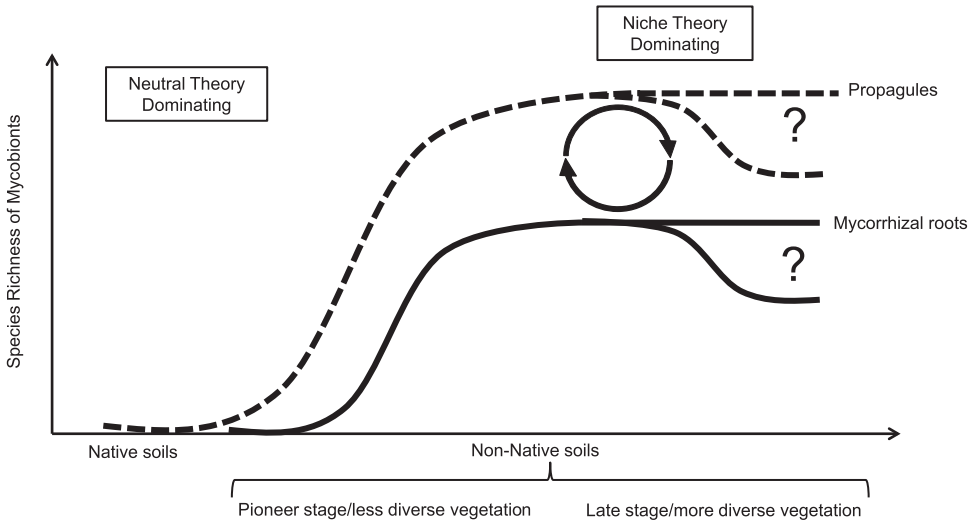

Fig. 3. Conceptual model of the dynamics of mycobiont species richness of both arbuscular mycorrhiza and ectomycorrhiza in ecosystems. The species richness of mycobiont propagules is always higher than the one on mycorrhizal roots. In native soils without any propagules, pioneer plants are non-mycorrhizal. During ecological succession on non-native soils (i.e. with a propagule pool), the mycobiont diversity increases and finally levels along succession stages and with plant species richness level. At late succession stages or plant diversity levels, the mycobiont diversity could also be expected to decrease.

low level diversity plots are often maintained by weeding, which can outcompete mycobionts sensitive to disturbance (Konig et al., 2010). At an initial stage of such experiments, it is evident that plant communities with higher diversity levels may recruit more diverse mycobionts due to their enlarged range of rooting depth and root traits but also of plant-plant interactions compared to plant species poor treatments (Toju et al., 2014). However, over a longer time span, mycobionts that are compatible with a broad range of root types should be privileged in the recruitment by plants so that one can hypothesize a reduction of the mycobiont diversity with time (Fig. 3). Consistently with this view, the diversity of mycobionts was shown to level in old plant communities (Wallander et al., 2010). However, the relationship between diversity of both partners of mycorrhizal communities is surely more complex. For example, replacing tree species rich pristine tropical forests by assemblages of lowered tree diversity had no real impact on the diversity of the mycobionts (Haug et al., 2013), which suggests that other factors than phytobiont diversity impact on mycobiont diversity, or that propagule banks display a kind of resilience. New generations of monitoring and experimental biodiversity analyses are required to unravel this complex relationship, and there is also a need of new approaches in the result analyses.

How do rare mycorrhizal partners survive?

Among such kinds of approaches, interaction network analyses have enabled to unravel the enigma posed by rare partners of mycorrhizal symbioses. As mentioned previously the frequency of mycobiont taxa typically follows a harp shaped pattern, with large numbers of rarely occurring taxa. It was long questioned how these rare taxa proceed not to extinct in competition with dominant mycobionts having higher probabilities to be recruited by new growing roots. According to the interaction networks theory, symbiotic organisms should follow a nested pattern, meaning that rare taxa only associate to frequently occurring partners for having a survival chance (Bascompte, 2010). Such nested pattern could be observed in case of mycorrhiza (Chagnon et al., 2012; Montesinos-Navarro et al., 2012). Another promising way is to realize co-occurrence analyses. It is established that single root tips colonized by several intermingled mycobionts are not rare in nature (Buscot, 1994). Co-occurrence analyses are frequently used in ecology (Bender et al., 1984; Gotelli, 2000) and have the power to depict groups of mycobionts which co-occur or, on the contrary, are excluding each other. Such co-occurrence analyses may introduce a new dimension in research on biodiversity of mycorrhiza. They invite to consider that mycorrhiza is definitively not a simple dual interaction between one mycobiont and one phytobiont, but between communities of both partners, and that within such communities, complex facilitation groups exist. Such facilitation groups encompass further groups of organisms than plants and fungi, as mycorrhizal associations are recognized to interact with manifold types of soil organisms (Fitter and Garbaye, 1994). Vice versa, mycorrhiza were demonstrated to have vertical effects on performance along as much as four trophic levels (Hempel et al., 2009).

Conclusion

In this article we review some traits of mycorrhiza as an example of symbiosis types that use the partner changing strategy to cope with the predicted instability of tight symbiotic associations (Boucher, 1985). As illustrated by the natural history of the two main mycorrhiza types, the arbuscular and ecto-mycorrhiza, this unstable kind of association gave rise to establishment to the huge evolutive diversification and today biodiversity of terrestrial plants. However, AM and EM took different ways. AM mycobionts are obligate biotrophs all belonging to a monophyletic group. Their relative low biodiversity might correspond to their specialization on simple mineral resource type. However, as they provide a crucial physiological advantage for plant nutrition, AM mycobionts triggered a dramatic ecological radiation of their partner, a trait that is encountered in many types of symbiosis (see discussion in Douglas, 1994). In contrast, the EM trait was acquired convergently within distinct soil fungi phyla. The high diversity of EM mycobionts provides the power of foraging heterogeneous and patchy distributed resources to a giant life form of plants (trees), but it did not contribute to a high biodiversity level of EM trees (Alexander and Lee, 2005).

Despite the different natural historic trajectories and physiological capacities of AM and EM mycobionts, the facts reviewed here indicate that both their diversity patterns in ecosystems and the mechanisms that regulate their diversity dynamics are pretty similar (see Fig. 3). In pioneer ecosystems, the limiting factor of AM

and EM mycobiont species richness is the import of propagules on native soil substrates. In developed plant communities, the highest mycobiont diversity is encountered within the propagule community, from which adapted dominant taxa are recruited by roots. However, the fundamental ecological sensitivity of symbioses does not permit a long term dominancy to the recruited mycobionts, as they are replaced by other dominants when ecological conditions change (e.g. seasonally or during plant succession). This turnover contributes to maintain a highly diverse propagule pool, whereby the role of permanently rare mycobionts on roots remains to be enlightened. In addition external import of propagules seems to help maintaining the richness level of mycorrhiza under each situation. A number of the actual analyses try to clear whether the neutral or the niche theory rule the occurrence and diversity of mycorrhizal mycobionts. A comprehensive study on AM (Dumbrell et al., 2010) showed species abundance to fit to the zero-sum multinomial distribution and observed certain propagule dispersal limitation, both facts supporting that the neutral hypothesis matters. However, the authors also found a strong response to soil abiotic niche factors such as pH and estimate these to be the principal determinant. An effect of pH and pH related soil factors was also found in a study comparing geothermal and non-thermal grasslands, while dispersal was not found to matter (Lekberg et al., 2011). Also the relation of seasonal AMF population dynamics to variations in the plant exudation pleads for a dominance of the niche in shaping arbuscular mycorrhizal communities (Dumbrell et al., 2011). Recently we participated to a study on EM in highly diverse subtropical forests with plots of different ages of regeneration. While environmental factors shaped the mycobiont community at all age stages, dispersal also had an influence but only in old plots (Gao et al., accepted). Based on the facts summarized here, we propose that the neutral theory will dominantly matter under pioneer situations on native soils, while the niche theory rather matters in established communities, but this balance may move again in older communities in which the diversity of the mycobionts may tend to drop (Fig. 3). Undoubtedly studies on larger space and time frames are needed to unravel this ecological point.

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